Insectes Sociaux
https://doi.org/10.1007/s00040-026-01106-9

Insectes Sociaux

RESEARCH ARTICLE

Pheromone trail following is not modulated by previous visit to food location, distance travelled, or travel direction in the ant *Lasius niger*

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Received: 19 September 2025 / Revised: 16 April 2026 / Accepted: 4 May 2026

Abstract

Ant foraging and recruitment often relies heavily on pheromone trails, and ants modulate pheromone trail deposition strategically. Ants are also known to modulate trail following depending on their own private information, such as the known location of the nest and their knowledge of food sources in the environment. Here we ask how a series of important context variables—distance from the nest, direction of travel, and prior food discovery—affects the fidelity of pheromone trail following in the black garden ant *Lasius niger*. Using both an open arena assay and a binary Y-maze design, we evaluated whether ants adjust their trail-following behaviour. Ants exhibited robust and consistent trail-following behaviour across all conditions. Surprisingly, we found no significant modulation by distance, travel direction, or recent experience. However, we observed that distance travelled before finding a pheromone trail significantly influenced subsequent walking patterns such as straightness, speed, and total distance travelled. These findings suggest that while *L. niger* trail-following behaviour is remarkably stable across contexts, locomotory traits remain plastic and context-sensitive. The decoupling of pheromone response from internal or external conditions highlights the need for further investigation into the mechanisms regulating individual foraging decisions in social insects.

Keywords Ants · Pheromone · Decision-making · Information use

Introduction

Pheromone use is widespread in insects, for a variety of purposes, such as attracting mates or signalling danger. Social insects stand out in the complexity of their pheromonal communication, where they are deployed for a wide range of purposes. Among those, perhaps the most studied are the pheromone trails of ants, which serve as both an attractant, inducing workers to start foraging, and as an orientator, giving the direction of the food source (Czaczkes et al. 2015). In some ant species, pheromone trails can lead to the mobilisation of thousands of workers in a couple of minutes, in a self-organised process called mass recruitment (Wilson 1962a). While this system is highly efficient at recruiting a high number of individuals to a food source, it might require modulation to adapt to changes in the environment (such as the discovery of a higher quality food source).

The flexibility (or lack thereof) of the trail pheromone system has been relatively well studied (reviewed in Czaczkes et al. 2015). At the collective level, many ant species have been shown to recruit more strongly to higher quality food sources (Wilson 1962a; Hangartner 1970; Jaffe and Howse 1979; Verhaeghe 1982; Jackson and Chaline 2007; Frizzi et al. 2018). Ants also recruit more strongly to larger food sources which they fail to move alone (Schatz et al. 1997; Robson and Traniello 1998; Czaczkes and Ratnieks 2012). At the individual level, pheromone deposition increases with starvation and with food quality (Hangartner 1969). Foragers have been shown to increase the number of pheromone depositions with increasing distance travelled (Beckers et al. 1992), and they might also be able to modify the quantity per deposition (Hangartner 1970). Since these

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pioneer experiments, evidence has accumulated to show that the modulation of the pheromone trail is driven by a very broad range of factors, related to the state and experience of the individual, the state of the colony, and the environment and state of the recruitment trail. In the ant *Lasius niger*, foragers must ingest a critical minimum volume to start the recruitment process (Mailleux et al. 2000), and this critical volume is larger in starved colonies (Mailleux et al. 2006). Previous experience also modulates pheromone laying: ants expecting high-quality food reduce recruitment to a moderate-quality food source relative to ants which expected a moderate-quality food source (Wendt et al. 2019). The objective food quality being held constant, pheromone deposition can also be modulated according to its perceived (subjective) value, such as the food source requiring more effort to reach (Czaczkes et al. 2018), being an expected flavour (Oberhauser and Czaczkes 2018), or being presented all together, as opposed to in multiple smaller resource units (De Agrò et al. 2022). However, other findings in the same species show that recruiters lay trail marks of equal intensity, whatever the number of food sources visited (Mailleux et al. 2003). Ants can deploy pheromone deposition strategically, in order to improve navigation on hard-to-learn paths (Czaczkes et al. 2013) or when it is dark (Jones et al. 2019), or when especially close to a food source (Devigne and Detrain 2006; Czaczkes et al. 2024).

In addition to modulation of the trail deposition, foragers also have the possibility to vary their propensity to follow the pheromone signals. Outside of trail pheromones, the response to alarm pheromone is stronger in older individuals in four ant species (Norman et al. 2017; Pokorny et al. 2020; Hart et al. 2024) and the honeybee (Robinson 1987). A recent study in the clonal raider ant revealed that this is due to some areas of the antennal lobe becoming more sensitized (Hart et al. 2024). Older *Myrmica rubra* workers follow pheromone trails more accurately (Cammaerts-Tricot and Verhaeghe 1974).

Pheromone following can be flexible and context dependant: ants can ignore pheromone trails in favour of following route memories, depending on the relative strength of the trail and the memory (Fourcassie and Beugnon 1988; Harrison et al. 1989; Grüter et al. 2011; Almeida et al. 2018). However, ants primed to expect the pheromone to lead to a better food source than the one they have been previously exploiting follow pheromone trails over route memories (Czaczkes et al. 2019). Ants can even learn to ignore pheromone when it consistently leads to unrewarded locations, although they cannot learn to avoid pheromone trails (Wenig et al. 2021). This could be explained by the fact that ignoring a cue is more challenging than associating it positively or negatively with a stimulus. Surprisingly, internal states have often not been found to modulate trail following. Whether an ant is a naïve scout, has been recruited, or has previously found food, did not influence their probability of following a trail pheromone on a T-maze (Czaczkes et al. 2017). Some species, such as *Monomorium pharaonis*, seem to have specialised 'pathfinders' which can find faint trails, follow them, and reactivate them (Jackson et al. 2006 a). However, by contrast no evidence could be found for specialised trail ignorers in the ant *Lasius niger* (Koch and Czaczkes 2021).

Ants thus appear to have the ability to modulate trail following, but do not do so in all circumstances in which they might be expected to. To get a deeper understanding of this question, examining pheromone following behaviour in a more complex setting than classical experiments may be helpful, allowing the scoring of more subtle behaviour than a simple binary response of the decision to follow or not the pheromone. In this study, we thus investigated the effect of context on the decision of an ant to follow a pheromone trail, but we also investigated how close the ants stayed to the trail in an open arena, and examined the ants' path characteristics. We explored the effects of distance travelled prior to encountering a trail in an open arena. We also measured the effects of travel direction and prior food discovery on trail-following in a more traditional Y-maze design. We hypothesise that ants that are further away from their nests will pay a higher cost for becoming lost, and thus should attend to pheromone trails more. Ants can estimate distances from the nest through optical flow (Ronacher and Wehner 1995) or the number of steps (Wittlinger et al. 2006). Similarly, we hypothesised that naïve ants heading away from the nest should follow pheromone trails with a higher fidelity than experienced ants which have already located a food source and are returning to it.

Methods

Ant collection and care

Lasius niger workers were collected on campus at the University of Regensburg. They were housed in plastic boxes with plaster of Paris nests and floor, and fed 0.5 M sugar water solution *ad libitum*, and chopped cockroaches three times a week. Each colony was kept for at least a week in the laboratory before being tested, in order to give them time to acclimatize. Colonies were queenless and comprised of ca. 500–1500 workers. The ants were starved 3 or 4 days prior to the experiments to ensure motivation to forage and explore. Data were collected between the 27th March and 5th of April 2024 for experiment 1, and between the 30th May and 12th of June 2023 for experiment 2. 6 colonies were used for experiment 1 and 8 for experiment 2.

Pheromone solution

Artificial pheromone was created by dissecting and macerating the trail pheromone glands (hindgut) of 4 individuals in 1 mL of Dichloromethane (DCM). 6 µl of such a solution over 10 cm results in a strong but ecologically sensible pheromone trail (von Thienen et al. 2014).

Experiment 1—Does distance from the nest on an outward journey impact pheromone following and exploration behaviour in an open arena?

The objective of the first experiment was to evaluate whether ants are more inclined to follow a pheromone trail encountered when they have already travelled far from their nests, compared to ants that have travelled only a short distance from the nest. In addition, we measured how path length and pheromone presence affected the exploration of the open arena.

- *Experimental procedure*: A single forager was allowed to walk onto a piece of paper and was placed on either a short path–20 cm long (and 1 cm wide) straight runway—or a 100 cm long runway. This method has been used previously by Poissonnier et al. (Poissonnier et al. 2023). At the end of the runway, a toothpick allowed them to climb vertically via a hole onto the centre of a paper-covered A4 platform (21 × 30 cm). A solvent (DCM) or pheromone trail (ca. 36 µl over 30 cm) was present, crossing the platform lengthwise and parallel to the path the ant came from (see Fig. 1). DCM and pheromone treatments were alternated between each ant. Ants' movement was video recorded with a raspberry pi high quality camera (12 megapixel, 25 frames per second) until it reached the border of the arena. Ants were discarded if they fell of the path (34/143 ants), crawled under the arena or took more than 20 min to reach the arena (2/143 ants). The setup was cleaned with ethanol and a fresh sheet of paper placed between each ant. Trials were video recorded from above. $N = 26$ ants per condition.

- *Analysis*: Ants were tracked with AnimalTA (Chiara and Kim 2023). For each video, we manually recorded the coordinates of the 4 corners of the A4 arena, which gave us a scale factor to calculate the area 1 cm on each side of the middle of the paper. All analyses were carried out in R (4.4.1)(R Foundation for Statistical Computing 2024) via Rstudio (2024.12.0). The number of ants exiting on the left vs. right side was compared with a binomial test. We ran linear mixed models to explore the effects of path length and pheromone trail presence on 5 variables of ant movement, using the lmerTest package (Kuznetsova 2017), with colony ID added as a random intercept effect. The variables were as follows: (1) The proportion of time spent in the central zone 1 cm on each side of the pheromone (or solvent) trail (see Fig. 1). (2) The average (mean) speed as the displacement speed between each frame where the target is considered as moving. (3) The total distance travelled (summed across all frames). (4) The time the ant took to reach the edge of the arena. (5) The straightness of the path, an index ranging between zero and 1 (0 less straight; 1 straight as a line), calculated by dividing the beeline from the first to last position of the ant divided by the total distance she travelled. Model

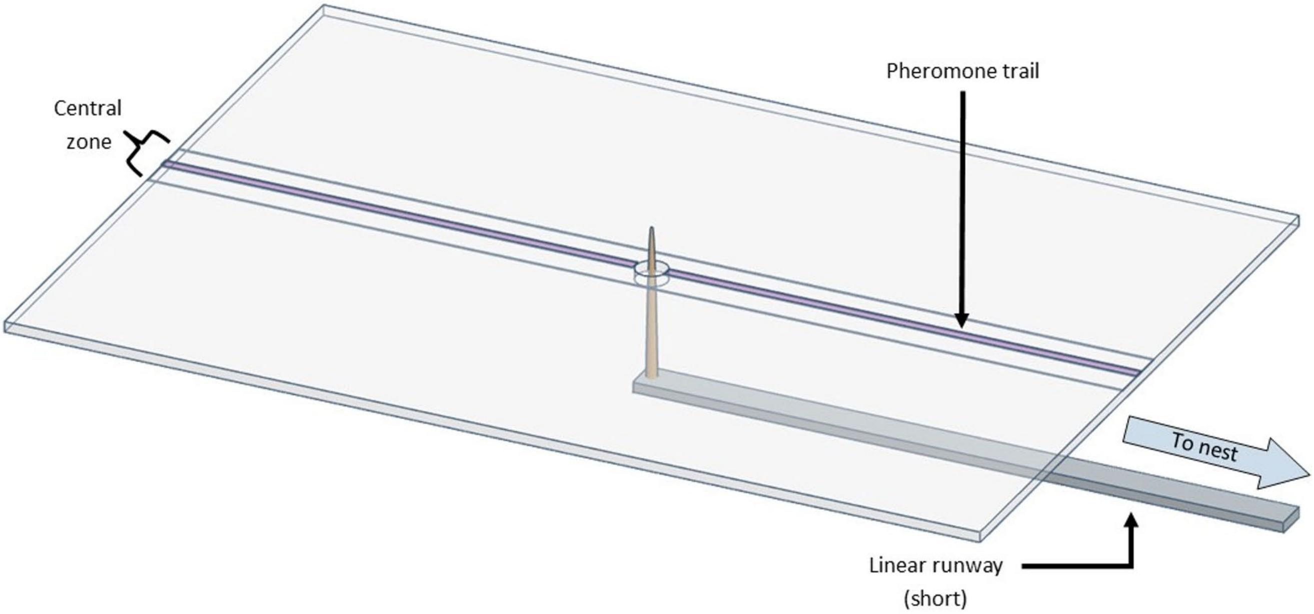

Fig. 1 Experimental setup for experiment 1, investigating the effect of path distance on pheromone following accuracy. Ants are placed at the end of the runway (short 20 cm shown, long 100 cm not shown), traverse the runway, climb up the central toothpick, and emerge onto the arena, covered with disposable paper and either a pheromone trail (shown) or a solvent control. Area is 297 × 210 mm (A4)

fit checks were performed using the DHARMa package (Hartig 2024). Except for speed and straightness, all data were log transformed to improve model fit.

Experiment 2—Does direction of travel and of food location impact pheromone following in a binary decision?

The aim of the second experiment was to ask whether ants are more inclined to follow pheromone trails when they are heading outwards in search of food, compared to when they are returning to their colonies. We additionally compared pheromone following of ants that have recently found a food source (a drop of 0.8 M sucrose solution) and were either returning satiated to the nest, or going outwards again in order to relocate the food source.

- *Experimental procedure*: The experimental procedure began with the lowering of a bridge leading to the Y-maze (2 arms 10 cm long, 1 cm wide, tapering to 2 mm at the bifurcation, coming together at a central bifurcation at a 120° angle). The ants experienced one of 4 conditions, all of which involve a Y-maze with a pheromone trail (6 µl solution over 10 cm) on one arm, and 6 µl DCM on the other:

(A) Outwards naïve: The ant walked outwards from the colony and was presented with a Y-maze.
(B) Outwards experienced: The ant walked outwards from the colony via a straight runway and found food (0.8 M sucrose) at the end of it. The ant was marked with paint while feeding and allowed to return to its colony. Once the ant had shared food with its nestmates, it was allowed to return to the setup, and was presented with a Y-maze.
(C) Return experienced: The ant walked outwards from the colony via a straight bridge and found food. It was marked with paint while feeding and allowed to return to share food in the colony. The ant returned to the food source and while eating the straight runway was replaced by a Y-maze, and the ant allowed to return nestwards via the Y-maze.
(D) Return naïve: The ant walked outwards from the colony via a straight runway and did not find any source of food at the end. While on a platform at the end of the runway, the runway was replaced with a Y-maze, and the ant allowed to return nestwards via the Y-maze.

Each protocol was carried out with the pheromone placed alternatively on the left or right arm of the Y-maze. Ants that did not reach the Y-maze, the food source, or the end of the straight runway in less than ten minutes were discarded. All overlays were removed, and the Y-maze, both straight runways, and the bridge were cleaned with 70% ethanol between each visit.

- *Analysis*: To test the effect of travel direction and experience on pheromone following we run a linear mixed model and attempted to predict whether the ant would follow a pheromone trail (1) or not (0) by the interaction of travel direction (outwards or nestwards) and experience (naïve or experienced), with the addition of the pheromone-marked side as another predictive variable, and colony ID as a random effect, varying by intercept and slope. A binomial error family was used with the package glmmTMB. $N=99$ or 100 per condition.

Results

The entire datasets for each experiment can be found as supplements and on OSF (link to experiments dataset). The entire analysis code and output can be found as supplement S2 and on OSF (link to code).

Experiment 1—Does distance from the nest on an outward journey impact pheromone following and exploration behaviour in an open arena?

Before exploring the effects of pheromone on movement data, we confirmed that the pheromone solution induced trail following in the ants, by checking if they stayed preferentially in the zone 1 cm on each side of the trail (Fig. 2). In Fig. 3, the position of the arena where the ants first reached a border is represented. We can see that when pheromone was present, most ants then exited the arena where the trail reached the border. When pheromone was absent, ants exited the arena more evenly. Indeed, the pheromone solution induced the ants to spend more time in the central zone 1 cm on each side of the pheromone trail the middle of the arena (Estimate = 0.1964, p-value < 0.01, Fig. 2, see also Fig. 4). There was no effect of path length (Estimate = 0.01462, p-value = 0.76) or interaction of path length and pheromone (Estimate = 0.01962, p-value = 0.77) on the time spent in this zone: ants who had travelled further away from their nests were not more likely to follow a trail they encountered on their path than ants which encountered a pheromone trail closer to their nests.

Walking speed was not significantly impacted by path length (Estimate = -2.784, p-value = 0.119). Ants coming from the short path had a mean speed of 23.5 mm s^{-1}, whereas ants coming from the long path had a mean speed of 26 mm s^{-1}. Surprisingly, the presence of pheromone did not increase walking speed. There was no effect of the interaction between path length and pheromone presence.

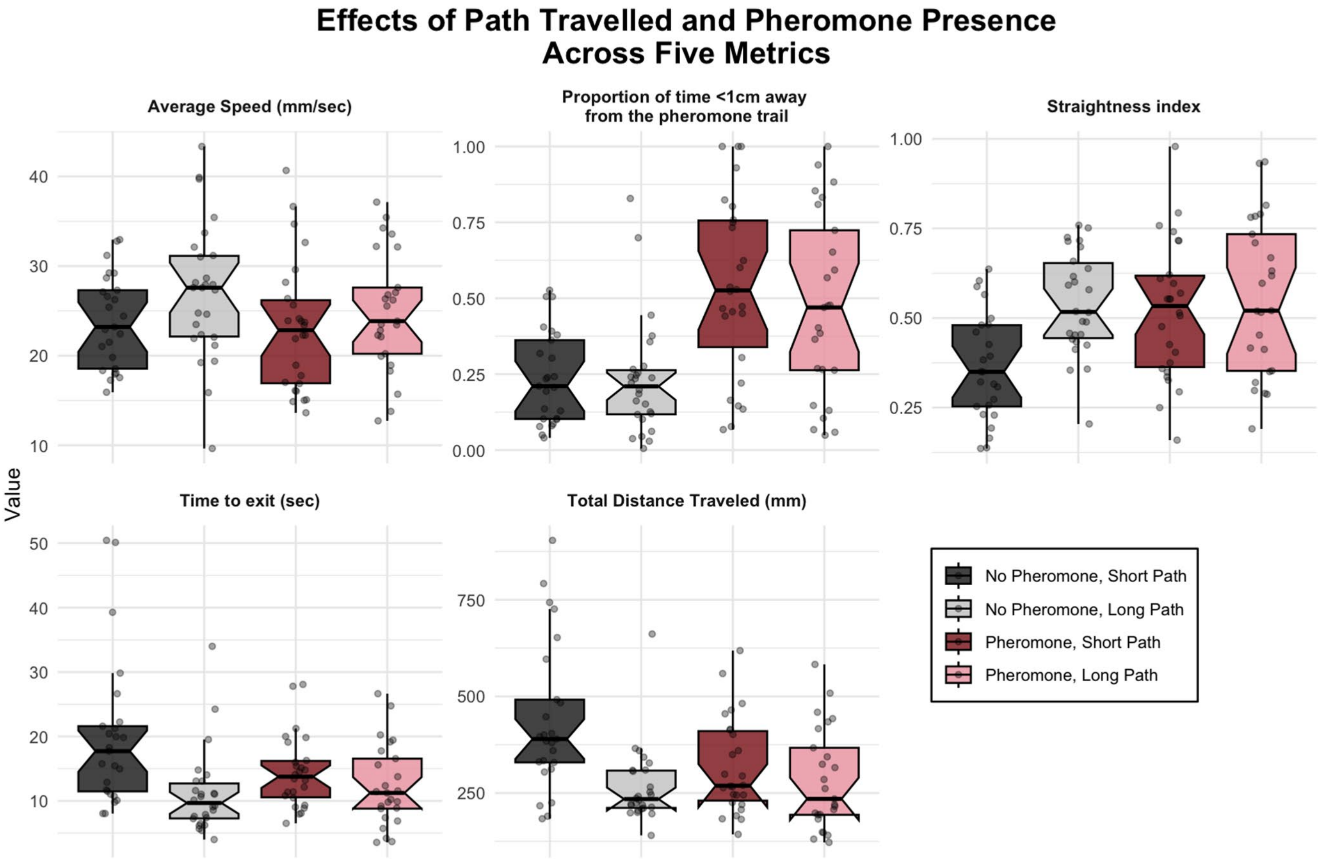

Fig. 2 Boxplots of 5 movement metrics for 4 conditions: the ants arrived on the platform from a short path (20 cm long), or a long path (0 cm long), and either solvent or a pheromone trail was present on the middle of the arena. The boxplots show the minimum and the maximum values, the median, and the first and third quartiles. Units are mm and seconds. $N = 25$ or 26 ants per condition

Straightness was affected by path length (Estimate = -0.6930, p-value < 0.01). When no pheromone was present, ants coming from the short path walked in a less linear trajectory (Fig. 2). Pheromone however did not impact straightness (Estimate = 0.12, p-value = 0.53). The interaction between the path length and pheromone was not significant (Estimate = 0.5479, p-value = 0.056).

Path length previously travelled affected the time to reach the border of the arena (Estimate = 0.56131, p-value < 0.01), ants coming from the short path took longer to exit the platform (mean for the short path 17.1, and 11.7 for the long path), likely due to their less linear trajectories noted previously. Pheromone did not have an effect (Estimate = 0.09103, p-value = 0.49). The interaction was close to significant (Estimate = -0.34158, p-value = 0.076).

Distance travelled on the arena was significantly impacted by previous path length (Estimate = 0.4593, p-value < 0.01): When no pheromone was present, ants coming from the short path travelled almost twice as much as the ones coming from the long path before reaching an edge of the arena (on average 501 mm vs. 266 mm, Fig. 2). Interestingly, this difference was reduced by the presence of the pheromone trail: the interaction between path length and pheromone was significant (Estimate = 0.31344, p-value = 0.04).

As an additional exploration of the data, we plotted the coordinates at which the ants exited the arena (Fig. 3). When pheromone trail was present, more ants exited the arena where the trail reached the edge of the paper. The number of ants exiting from the nest or opposite side was not significantly different (36 vs. 30 respectively, p-value = 0.5386).

Experiment 2—Do ants follow pheromone trails more accurately when returning to the nest?

There was no effect of travel direction, experience, or the interaction of travel direction and experience, on pheromone following accuracy (all $X^2 < 0.38$, all $P > 0.54$, see Fig. 5). The side of the Y maze on which pheromone was placed did not affect pheromone following (X2 = 2.19, $P = 0.14$). Overall, 87.4% of ants followed the pheromone trail (348 / 398).

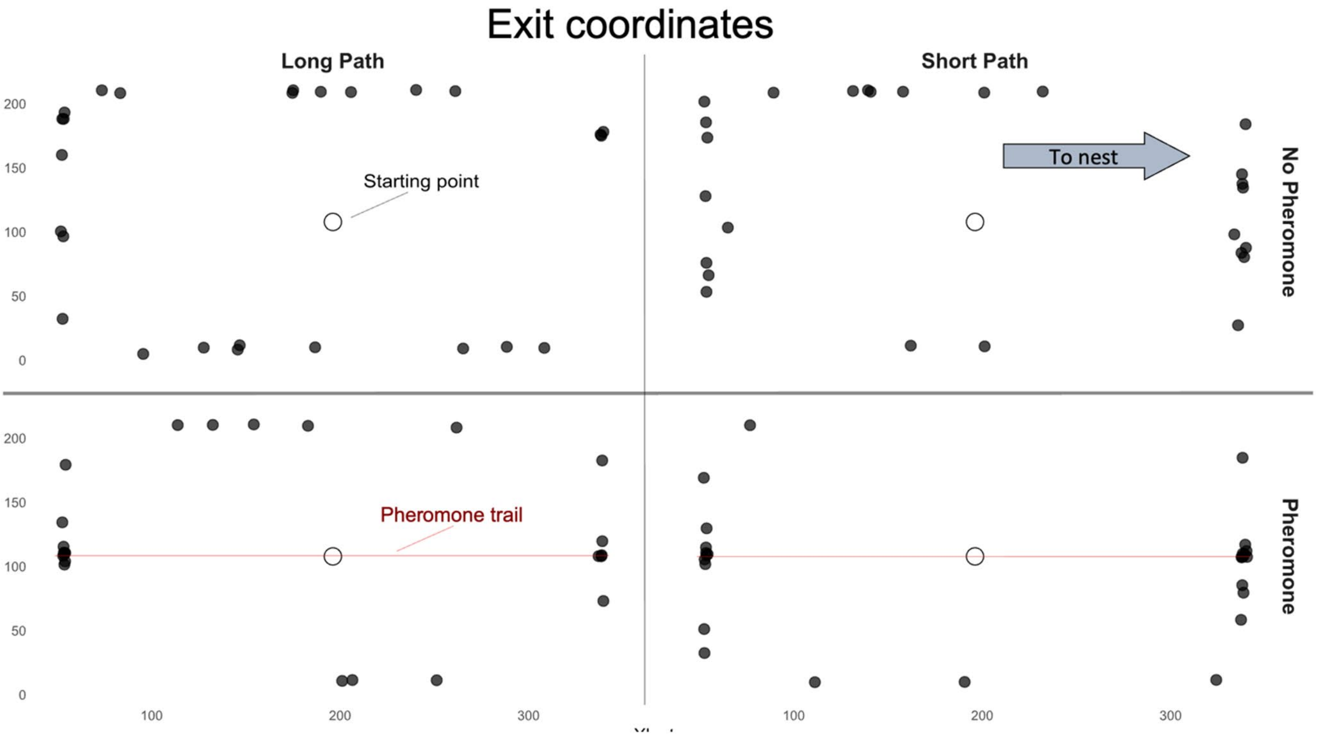

Fig. 3 Exit coordinates of ants per condition (mm), each dot representing an individual ant. The top panels represents where the ants reached one of the A4 arena edges when no pheromone trail was applied. The bottom panels represent the same data for ants that encountered a pheromone trail deposited in a horizontal line crossing the entrance point. The trail was parallel to the path the ants were coming from. The left panels show ants which travelled 20 cm to reach the entrance point (short path), the right panels ants which travelled 100 cm to reach the entrance point

Discussion

The trail following fidelity of *Lasius niger* appears to be quite resistant to task state, travel direction, and distance from the nest. We expected more pheromone following further from the nest, as the further from the nest, the more errors can accumulate and the more costly it is to get lost. We also expected more pheromone following going outwards than inwards for naïve ants because returning ants have information (where is nest) and outgoing ants do not know where food will be found.

However, we found that pheromone following in a Y-maze did not differ between outward and return trips to the nest, nor was it affected by whether food had been encountered on the previous trip. Similarly, Czaczkes et al. (2017) reported that *L. niger* foragers in a T-maze showed no change in pheromone-following behaviour regardless of whether they were naïve, recruited, or experienced. Several factors may explain this absence of effect. One possibility is that the ants had no strong incentive to favour one branch over the other, since they had not experienced the alternative branch as unrewarding. Perhaps had there been some conflict (pheromone pointing further away from the nest-food axis, for example), or a more complex path, we would have seen differences between treatments, as outgoing experienced foragers rely on memory more than outgoing naïve ants. In addition, there is some evidence that ants can monitor their own uncertainty (Merkle and Wehner 2010; Czaczkes and Heinze 2015) and the uncertainty in their path integration system (Merkle and Wehner 2010). Since the ants were restricted to a linear runway, they may not have accumulated sufficient noise in their path integration system to cause a detectable change in behaviour, and there may not be a strong cost of not following the pheromone.

In order to complement the Y-maze experiments, in this study we also looked at trail following in an open arena, which could allow us to detect more subtle differences in trail following that might not be apparent in the Y-maze. In the open arena, we found that distance travelled before encountering the pheromone trail did not affect the ant's trail following accuracy. In an older study in *Solenopsis saevissima*, deviation of trail following did not vary with distance along a 10 cm long trail in (Wilson 1962b), pointing to similarities with *L. niger*. However, we did find effects of the distance travelled on the walking behaviour of the foragers, with ants having walked a longer way having a more linear trajectory.

Could the lack of effect of distance travelled be due to ants not being able to perceive the difference between 20

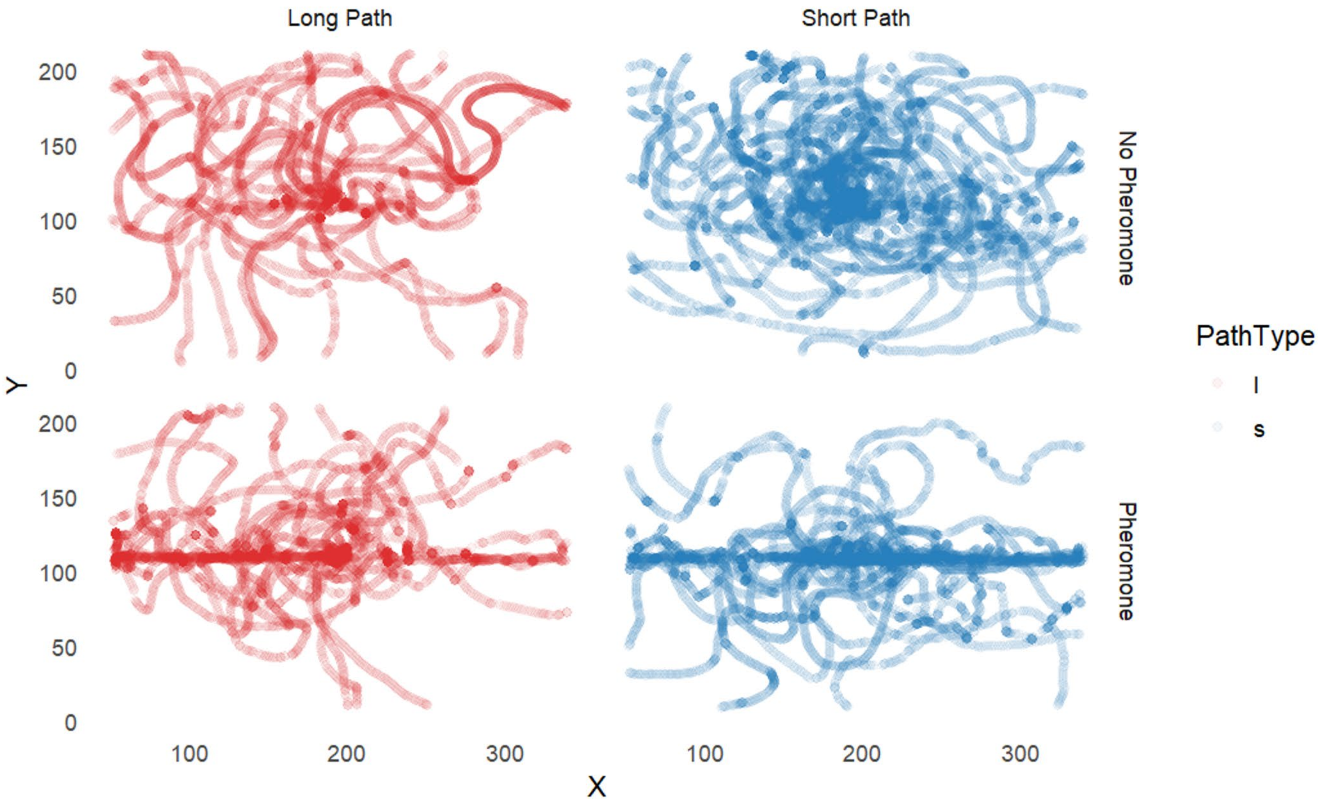

Fig. 4 All coordinates of all ants in each condition (long path of 100 cm or short path of 20 cm, pheromone or control DMC horizontal line drawn in the middle of the A4 paper)

and 100 cm? It appears more likely that pheromone following responds to different rules than pheromone deposition. Indeed, in the same species and with the same path length (20 vs. 100 cm), we found that foragers deposited more pheromone to food sources that were more distant from their nest (Czaczkes et al. 2024), a finding which replicated previous similar findings using a different setup (Devigne and Detrain 2006). Ants are therefore able to detect differences in the range of distance we used.

Why would pheromone information provision rules differ from pheromone following rules, when both have the same goal? Perhaps the costs of not depositing pheromone and not following pheromone are under different constraints. For instance, if the ant decides not to lay pheromone, the direct costs at the individual level might be minimal, as the ant can still remember the way to the food. However, the costs could be high at the collective level, as other ants will not be directed to the food source, which could be quickly monopolised by another colony instead. On the other hand, the decision not to follow the pheromone could affect the individual level more directly, through the costs of exploring unknown territory or getting lost for example, leading to less flexibility in pheromone following.

This study demonstrates a remarkable robustness in trail pheromone following decisions (c. 85%) in an ant, which is not due to ceiling effects (where increasing the concentration of pheromones would no longer increase attraction), and unlikely to be due to limitations on detection. This replicability in pheromone following proportion is echoed in previous studies too. Taken together, it is clear that pheromone following probability is stable, and not set at 100%. The question which remains is: why is this, and do these results translate to other contexts and uses of pheromone? Would ants which are recruiting to a nest site after their nest has been destroyed follow pheromone trails with greater fidelity? Or perhaps would starving colonies follow pheromone trails with more fidelity, given that finding other food sources seems unlikely? A system with a stable proportion of pheromone followers and some variation in the pheromone laying might allow the colony to have a balance between flexibility and quick efficient recruitment to a food source, while relying on simple rules at the individual level. The flexibility of pheromone following in a variety of contexts outside foraging for sucrose awaits further exploration.

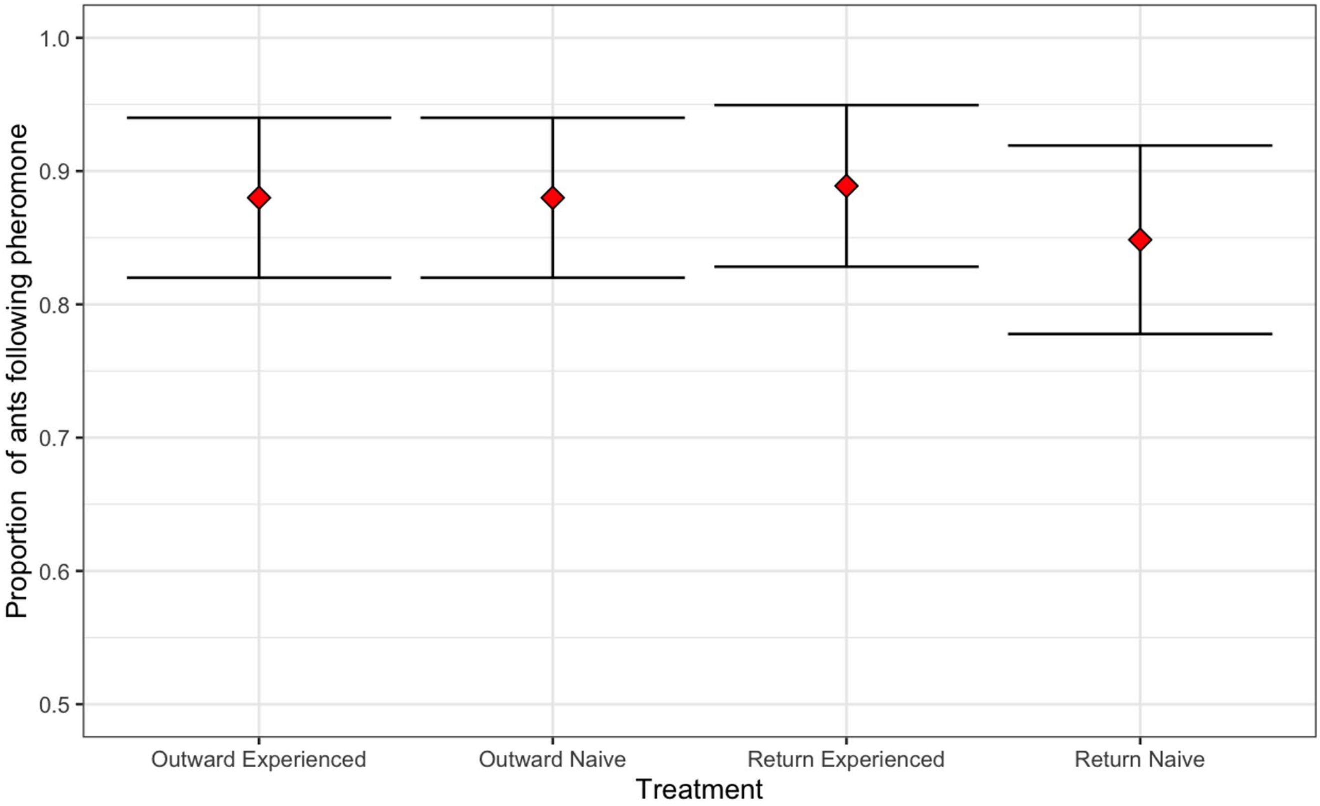

Fig. 5 Proportion of *L. niger* foragers that followed pheromone in a Y-maze where one branch presented pheromone, and the other the solvent only. The choices of the ants were recorded in 4 different situations. The Y-maze was presented either on the way out of the nest—Outwards, or on the way back to the nest–Return. In addition, the ants either experienced a food reward—Experienced, or did not—Naïve condition. The red diamonds represent the mean, and the error bars are 95 bootstrap confidence intervals. $N=99$ or 100 ants per condition

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00040-026-01106-9.

Acknowledgements L-A. P. was supported by an Alexander von Humboldt Postdoctoral Fellowship (1223114) at the beginning of the project, then by a Postdoctoral Equal Opportunities Fellowship from the University of Regensburg. T.J.C was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Project No. 462101190.

Funding Open Access funding enabled and organized by Projekt DEAL.

Declarations

Conflict of interest We declare no competing interests.

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